



UNIVERSITY OF QUEENSLAND
PAPERS

DEPARTMENT OF BOTANY
(PREVIOUSLY DEPARTMENT OF BIOLOGY)

Volume III.

1954

Number 7

The Origin and Differentiation
of *Claviceps* Species

By

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DATE OF PUBLICATION:
29th DECEMBER, 1954

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Wholly set up and printed in Australia by
WATSON, FERGUSON AND COMPANY
Brisbane, Q.

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THE ORIGIN AND DIFFERENTIATION OF *CLAVICEPS* SPECIES

By R. F. N. LANGDON, M.Agr.Sc., Ph.D.

The genus *Claviceps* is of very wide distribution, being recorded from all continents, and from equatorial regions to high latitudes. The species of *Claviceps* have a specialised habit, being parasites in the ovaries of grasses and sedges. With the exception of a few species the cycle of development of the ergot fungi exhibits two distinct phases—(a) a period of independent existence, (b) parasitic development on a living plant.

The period of independent existence is largely one of dormancy, when the sclerotia lie on the ground or amongst plant debris, exposed to a fluctuating environment, mainly in regard to temperature and moisture. The latter part of this period is an active one, with the development of ascostromata and maturation of ascospores. This state of development of the fungus is perhaps its most precarious one, for it is at this time small and delicate and yet subject to all the vagaries of its environment. In their parasitic phase, the ergot fungi find a relatively uniform habitat. Their nutrients are drawn from the host, and their thalli are protected by the glumes of the spikelets.

In the evolution of the species of *Claviceps* morphological differentiation has resulted in an assemblage of fungi which are distinguished from one another by the relative shape, size, colour and arrangement of various structural and reproductive parts. Morphological features are but one aspect of any group of parasitic fungi, and can be regarded as only the visible evidence of variation within a group. Concurrently with morphological changes there have undoubtedly occurred alterations in the fungi which have a physiologic basis. The development of a wide host range by fungi must suppose changes in both hosts and fungi which permit a satisfactory mutual interaction, *i.e.*, any host specialisation by fungi is the result of physiological evolution. Such changes in *Claviceps* species would be indicated by the nature of their host range. Even if a species of *Claviceps* can establish a parasitic relationship with the host plants available to it, there is also the necessity for that fungus to withstand the vagaries of the climate while it lies dormant in its sclerotial state, and also for it to be subjected to conditions which eventually will result in its giving rise to ascostromata. Ecological evolution, as well as morphological and physiological evolution, must therefore be considered as processes involved in the differentiation of the species of *Claviceps*.

The Species of *Claviceps*

Langdon (1952) in a survey of the species of *Claviceps* concluded that 25 species are known, and that further investigations on ergot in tropical regions might reveal others. *C. maximensis*, described recently from Africa, brings the total to 26. The species now recognised are:

- Claviceps purpurea* (Fr.) Tul. Ann. Sci. Nat. Ser. iii, 20, 45, 1853. Syn. *C. microcephala* (Wallr.) Tul.;
C. setulosa Quel.; *C. sesleriae* Stager.
Claviceps nigricans Tul. Ann. Sci. Nat. Ser. iii, 20, 51, 1853.
Claviceps pusilla Ces. Comment. Soc. Crittog. Ital. 1, 64, 1861.
Claviceps uleana P. Henn. Hedwigia 1899, p. 64.
Claviceps lutea Moller. Phyc. u. Ascom, Bras. 305, 1901.

- Claviceps ranunculoides* Moller. Phyc. u. Ascom. Bras. 305, 1901.
Claviceps cinerea Griff. Bull. Torr. Bot. Club. 28, 236-240, 1901.
Claviceps paspali Stev. & Hall. Bot. Gaz. 50, 462, 1910. Syn. *C. rolfsii* Stev. & Hall.
Claviceps tripsaci Stev. & Hall. Bot. Gaz. 50, 463, 1910.
Claviceps flavella (Berk. & Curt.) Petch. Trans. Br. Myc. Soc. 18, 28, 1933. Syn. *C. pallida* Pat.; *C. patonillardiana* P. Henn.; *C. balansioides* Moller.
Claviceps yanagawaensis Togashi. Trans. Sapporo Nat. Hist. Soc. 14, 281, 1936.
Claviceps argitariae Hansford. Proc. Linn. Soc. London, 1940-41, p. 37.
Claviceps annulata Langdon. Proc. Roy. Soc. Qld. 54, 26, 1942.
Claviceps hirtella Langdon. Proc. Roy. Soc. Qld. 54, 27, 1942.
Claviceps platytricha Langdon. Proc. Roy. Soc. Qld. 54, 27, 1942.
Claviceps glabra Langdon. Proc. Roy. Soc. Qld. 54, 28, 1942.
Claviceps grohii Groves. Mycologia 35, 604-609, 1943.
Claviceps viridis Padwick & Azmat. Curr. Sci. 12, 257, 1943.
Claviceps litoralis Kawatani. Bull. Imp. Hyg. Lab. 65, 81-83, 1944.
Claviceps diadema (Moller) Diehl. Agr. Monogr. No. 4 U.S.D.A., p. 60, 1950.
Claviceps orthocladae (P. Henn.) Diehl. Agr. Monogr. No. 4 U.S.D.A., p. 60, 1950.
Claviceps inconspicua Langdon. Proc. Roy. Soc. Qld. 61, 31, 1950.
Claviceps maximensis Theis. Mycologia 44, 792, 1952.
Claviceps sulcata Langdon. Univ. Qld. Papers (Botany), 3, 4, 39, 1954.
Claviceps cynodontis Langdon. Univ. Qld. Papers (Botany), 3, 4, 39, 1954.
Claviceps queenslandica Langdon. Univ. Qld. Papers (Botany), 3, 4, 39, 1954.

The imperfect states of *Claviceps* show considerable variation, especially the sclerotial state. Three distinct types of sclerotium have been noted. The first is that termed here the balansioid type, found in *C. diadema* and *C. flavella*, where the mycelium binds together parts of the spikelet additional to the ovary to give a structure reminiscent of the pseudosclerotium of the genus *Balansia*. The second group are those sclerotia which are subglobose, and usually light coloured. *Claviceps paspali*, *C. queenslandica*, *C. lutea*, *C. hirtella* and *C. orthocladae* belong to this group. The third group are elongate forms, ranging from ovoid and somewhat pointed through clavate and corniform to long fusoid-cylindric. The sclerotia of this group are dark-coloured. Of these groups, the first may be regarded as the most primitive, with less specialisation of the fungus in regard to the tissues it invades and the lack of clear-cut and definite sclerotial form. The second group may be regarded as more specialised in that growth is restricted to a single organ, the ovary. But the subglobose form and light colour suggest only a heaping up of mycelium within approximately the limits of the ovary. In contrast to this, the sclerotia of the third group exhibit intercalary growth as indicated by the presence of stigmatic tissues at the distal ends of long sclerotia. The species of this group are regarded as the most advanced ones, morphologically.

The conidia of *Claviceps* species vary considerably in shape and size, and for some species these features are often quite distinctive. The very small conidia of *C. diadema*, the distinctly 3-sided outline of the conidia of *C. pusilla*, the arcuate outline of several species associated with hosts from the tribe Paniceae, e.g., *C. hirtella*, *C. glabra*, *C. digitariae*, the reniform outline found in *C. cynodontis*, and the allantoid form in *C. sulcata* exemplify the variation that may be found. The dimensions of conidia, within a species, are variable, but the range of size is a useful character as an accessory to shape in the delimiting of species.

The perfect states developed from the sclerotial tissues are not, if considered alone, distinguishable from those of some other genera, such as *Balansia*, *Balansioopsis* and *Atkinsonella*. Within the genus *Claviceps* there are variations which aid in delimiting species of *Claviceps*. The colour of the ascostromata, though sometimes variable, is in many species a constant distinctive feature. The general ornamentation of the ascostromata is also a useful character for distinguishing between some species in this state of development.

Host Relations

The species of *Claviceps*, as a whole, have a very wide host range. Some species are found on only one host genus, others may be restricted to a particular tribe, and others still may range over the members of several tribes. An obvious explanation for any apparent specificity of an ergot to a host or group of hosts might be that various authors, consciously or not, have described as a new species any ergot that they encountered on a previously unrecorded host genus. But this is not what has happened. There are distinct morphological differences between species of *Claviceps*. The fairly restricted number of ergot species that are known (twenty-six) is in sharp contrast to the number of genera of hosts from which known species of *Claviceps* have been reported (over eighty).

A general summary of the host relations of *Claviceps* spp. is given here. It is based on an unpublished Host Index prepared by the author after an exhaustive survey of the literature.

GRAMINEAE

Pooideae:

Centothecae: *C. orthocladae*

Bambuseae, Brachypodieae, Glycerieae, Bromaeae, Seslerieae, Meliceae, Festuceae, Stipeae, } *C. purpurea*

Arundineae, Nardeae, Avencae, Danthonieae, Phalarideae, Agrostideae, Spartineae

Hordeae: *C. purpurea*; *C. litoralis*.

Chlorideae: *C. cynodontis*.

Zoysiaeae: *C. cinerea*; *C. yanagawaensis*.

Panicoideae:

Paniceae: *C. diadema*; *C. digitariae*; *C. flavella*; *C. glabra*; *C. hirtella*; *C. paspali*; *C. queenslandica*; *C. lutea*; *C. ranunculoides*; *C. sulcata*; *C. uleana*; *C. viridis*; *C. maximensis*.

Andropogoneae: *C. annulata*; *C. inconspicua*; *C. platytricha*; *C. pusilla*.

Maydeae: *C. tripsaci*.

CYPERACEAE

Carex: *C. grohii*.

Eleocharis, *Scirpus*: *C. nigricans*.

Only six ergot species are known on grasses of the Pooideae, four of which have a monogeneric host range. These are *Claviceps cynodontis* on *Cynodon* spp., *C. cinerea* on *Hilaria* spp., *C. yanagawaensis* on *Zoysia japonica* and *C. orthocladae* on *Orthoclada* sp. These ergot species are all quite distinct from one another. *C. purpurea* and *C. litoralis* are two very similar species, and are maintained as distinct in this paper with some doubt. *C. litoralis* has been described recently from Japan with *Elymus* and *Hordeum* as its hosts. *Claviceps purpurea* has a very wide host range, covering 50 genera distributed among 17 tribes, all from the subfamily Pooideae. No authentic record of *Claviceps purpurea* on a panicoid host has been found, and the few published reports of such an association appear to have been arbitrary determinations based only on the observation of imperfect states of ergot. The fact that the pooid hosts of *Claviceps purpurea* are the dominant members of the grasslands in regions where that fungus occurs may be noted here, but that alone does not seem to explain the absence of infection in panicoid grasses. There are panicoid genera in the areas of pooid dominance, and also, *Claviceps purpurea* has been introduced into areas where panicoid grasses are relatively abundant, yet no occurrence of that ergot on panicoid grasses seems to have resulted. The conclusion that *Claviceps purpurea* is restricted to the Pooideae because of some basic physiologic factors affecting its parasitism may be drawn from this observed host range. That certain

specialised parasites of grasses are restricted to particular groups within the family has been demonstrated by Favret (1949). From an analysis of the host relations of four cereal rusts, *Puccinia coronata*, *P. graminis tritici*, *P. graminis secalis* and *P. graminis avenae*, he concluded that these fungi had the capacity to infect only festucoid genera of grasses with a basic chromosome number of 7.

Although *Claviceps purpurea* has a wide host range, there is known to be some degree of specialisation within the species. Early in the century, Stager found several physiologic races with somewhat restricted host ranges. Stager's work has been summarised by Barger (1931).

Among grasses of the tribe Paniceae there are many genera from which species of *Claviceps* have been described. These ergots are undoubtedly distinct, and are apparently specific to rather narrow groups of hosts. *Claviceps hirtella* occurs in Queensland on *Eriochloa*, *Paspalidium* and *Brachiaria*, but not on other genera of the tribe Paniceae or of other tribes. Yet there has been ample opportunity for infection of other grasses in the field were those grasses susceptible. The inference must be that this ergot is specialised in its parasitism and, in South Queensland, finds only the genera mentioned to be suitable substrata. The ergots of *Digitaria* spp. in Australia and Africa are apparently confined to that genus, while the widespread and well known *Claviceps paspali*, though having a wide range of host species, has not yet been recorded from any genus other than *Paspalum*. There is evidence that the species of *Claviceps* associated with a particular genus of hosts is not the same everywhere. The ergots of *Digitaria* and of *Brachiaria* in Africa are different species from the ergots occurring on species of these genera in Australia, and more than one species of *Claviceps* has been described from *Panicum* in the New World. These facts suggest that while there is a general susceptibility to ergot among the grasses of the Paniceae, the development of species of *Claviceps*, i.e., forms that are morphologically different, has occurred, rather than the development of physiologic races, which has been the tendency with *Claviceps purpurea* among the Pooideae.

Several species of *Claviceps* have been found on grasses of the Andropogoneae, but except with *Claviceps pusilla*, there is no knowledge of their extra-Australian distribution and host range. But there are records of sphaelial parasites on some of the host genera in other areas, e.g., on *Ischaemum* in Asia, on *Hyparrhenia* in Africa and South America. *Claviceps pusilla*, widespread in the warmer parts of Europe, Asia and Australia, has been recorded on seventeen species from seven genera of the tribe Andropogoneae. The conidia of this ergot are of characteristic shape, and there is no suggestion from any source that hosts outside the Andropogoneae are ever infected, even though there are numerous tropical grasses known to have sphaelial parasites. In Queensland, in areas where the ergot has been abundant at times, no evidence of its spread to grasses other than Andropogoneae, or even to all genera of that tribe in the immediate vicinity, has ever been observed. *C. pusilla* appears to be restricted to certain genera of the sub-tribe Andropogoninae.

The general restriction of certain species of *Claviceps* to particular host taxa is illustrated below. The classification of the Andropogoneae used is taken from Stapf, in Flora of Tropical Africa, 9.

Andropogoneae

- Saccharinae—Pollinastrae—*Eulalia*: *C. annulata*.
 Ischaeminae—*Ischaemum*: *C. platytricha*.
 Andropogoninae: Hyparrhenastrae—*Hyparrhenia*: *C. inconspicua*.
 Sorghastrae—*Vetiveria*: *C. pusilla*.
 Amphilophastrae—*Capillipedium*: *C. pusilla*.
 Dichanthium: *C. pusilla*.
 Bothriochloa: *C. pusilla*.
 Andropogonastrae—*Cymbopogon*: *C. pusilla*.
 Heteropogonastrae—*Heteropogon*: *C. pusilla*.
 Themedastrae—*Themeda*: *C. pusilla*.

That four distinct species of *Claviceps* occurring in south-eastern Queensland should be restricted in this way to hosts which are distinct but related entities seems to be due to more than chance. It does support a hypothesis of concurrent morphological and physiological evolution.

Ecological Differentiation

Species of *Claviceps* occur in all continents, and in areas which differ very markedly from one another in climate. Although some tropical areas may have a uniform climate, allowing the hosts for ergot fungi to flower during most months of the year, most regions experience environmental fluctuations which lead to periodicity of flowering of the grasses. The cold winters of temperate areas are periods of host dormancy.* In many tropical and sub-tropical areas there are wet and dry seasons which influence the hosts' development, and temperature also may be effective, as it is in southern Queensland, where many grasses fail to respond to rain which may fall in winter. The various influences which determine the flowering periods of the grasses also effect ergot fungi which in the absence of inflorescences lack substrata for their parasitic phase. The ergots exist in the sclerotial state during the periods of dormancy of the hosts, and in this state are subject to the same environmental factors as have affected the hosts. The important factors concerned here are temperature and moisture, either singly or in combination.

The conditions to which the sclerotia of *Claviceps purpurea* must be subjected during their dormant period in order to ensure ascostromatal development later on have been investigated by Kirchoff (1929). He found that greatest development of ascostromata occurred with sclerotia which had been held for a minimum period of 25 days at a temperature of 2–3° C. Other workers (Petch 1937; Schwarting and Hiner 1945; Brentzel 1947), have confirmed the beneficial effect of low temperature on subsequent development of sclerotia. For germination of the sclerotia and development of ascostromata, several workers are agreed that moderate temperatures, between 9 and 15° C., are most suitable (Krebs 1936; Vladimirsky 1939; Brentzel 1947), and Krebs (*loc. cit.*) has found that these processes are checked at temperatures above 18° C.

Griffiths (1901) observed that sclerotia of *Claviceps cinerea* from *Hilaria* would, in contrast to those of *C. purpurea*, germinate almost at once if placed on moist sand after they were collected from the host plant. *Hilaria* is a small genus occurring in arid regions.

* For convenience in this discussion, dormancy of the host is taken as its non-flowering period, when the host is inactive in the sense that it does not then provide a substratum for ergot.

Griffiths considered this ergot to be adapted to arid conditions so that moisture supply rather than other factors determined when the sclerotia would germinate.

The effect of temperature on sclerotia of *Claviceps pusilla* was studied by Langdon (1950). Ascstromata developed in the spring just as abundantly on sclerotia subjected to temperatures of 2-3° C. for up to six weeks as they did on sclerotia kept at temperatures not below 10° C. throughout the winter. Low temperatures were not harmful to the sclerotia, but were not a pre-requisite to subsequent ascostromatal development, a point of interest in view of the tropical distribution of *C. pusilla*.

In two South American species, *Claviceps diadema* and *C. orthocladae*, ascostromata develop while the sclerotia are still in the inflorescence of the host. This condition is a feature of the genus *Balansia*, with which *C. diadema* was originally placed. But since infections with *Claviceps* species are localised in, and destructive to, the ovary, in contrast to the systemic endophytic habit of the *Balansias*, which infect a new generation of hosts through the seed of the previous generation, the biologic significance of this parallel development is different for *Claviceps*. Only when new host inflorescences were available at fairly short intervals throughout the year could an ergot with this balansoid character maintain itself. A fairly uniform climate, without extremes which would cause long periods of dormancy in the host, would be a pre-requisite to survival of such ergots, and it is interesting to note that the hosts of these ergots, *Icnanthus*, *Panicum* and *Orthoclada* are inhabitants of tropical forests and forest margins which provide the requisite conditions.

Our knowledge of the environmental conditions most suitable for the independent phase of the life cycle of *Claviceps* species is yet rather elementary, and the majority of the species have never been investigated. What information is available does indicate that evolutionary processes have sifted out the species which are well suited to certain environments. The ecological evolution of these species in their independent phases has no doubt a physiological basis in the sclerotia themselves, so that the general physiological evolution in the genus may be regarded as the result of selection through environmental reactions on the one hand, and through host-parasite interactions on the other.

Discussion

The Fungi are a group with a long history, and there is palaeontological evidence of their existence long before the development of Angiosperms. Possibly the ancestral grasses had ergot-like parasites, and the ergots of the present day evolved contemporaneously with their hosts. The species of *Claviceps* are a group morphologically distinct from one another. Each species has a well defined host range. There is also evidence of differentiation from an ecological viewpoint. Consideration of the evolutionary development of the Gramineae, the chief hosts of ergot fungi, may throw light on the origin and development of *Claviceps* species.

Bews (1929) regarded moist tropical vegetation as having had the longest continuous unchanging history. It has become highly differentiated and many types have been derived from it as a response to cooler and to drier conditions. The grasses of tropical and sub-tropical moist forest areas are the most primitive both floristically and ecologically. The most primitive of the Bambuseae, the Centothecaeae (including *Orthoclada*) and various other relatively primitive members of tribes of the Pooideae occur here. In the panicoid series, such genera as *Icnanthus*

and *Oplismenus* are typical forest types, and representatives of genera which are more characteristic of stream and river bank habitats, e.g., *Panicum*, *Paspalum*, *Brachiaria*, also occur in the forest habitat.

Marsh and stream bank hygrophilous grasses connect with forest margin types but tend to become much more widespread. In warm regions many genera of the Paniceae and some of the Andropogoneae are represented. The hygrophilous grasses of temperate areas are the relatively primitive tribes, and genera of the Pooideae, e.g., Festuceae, Glycerieae, and Agrostae. *Icnanthus*, *Panicum*, *Echinochloa*, *Paspalum*, *Paspalidium*, *Oplismenus*, *Setaria* and *Brachiaria* are genera of the Paniceae which are common in this habitat, while the pooid genera include *Poa*, *Festuca*, *Glyceria*, *Fluminea*, *Calamagrostis* and *Agrostis*.

The grasses of deciduous woodlands in temperate areas show a slight advance on those of tropical forests, genera of the Festuceae and the Agrostae being prominent. In regions of evergreen sclerophyllous vegetation the grasses show a considerable degree of advance and the Aveneae, Hordeae, Phalarideae and advanced members of other tribes are the chief components.

The Andropogoneae, a floristically advanced tribe, is poorly represented in the more primitive habitats, the moist forest, forest margins and stream-banks, but reaches its greatest development in tropical and sub-tropical savannah.

The abundance of species of *Claviceps* occurring in the tropics and sub-tropics relative to the number of species in temperate areas is a striking feature. The more primitive species of *Claviceps* with balansoid characters—sclerotia involving tissues of the spikelet beyond the confines of the ovary, and development of ascostromata while the sclerotia are still on the host, are those found on grasses which Bews regards as primitive both in their morphology and their habitat. Thus we find *Claviceps orthocladae* on *Orthoclada* (Centothecae), *C. diadema* on *Icnanthus* and *Panicum*, and *C. flavella* on *Echinochloa*, these hosts all being shade loving or hygrophilous and relatively primitive panicoid types. Ecologically as well as morphologically, these *Claviceps* species may be regarded as primitive, for they are in close relation to the living host in all stages of development, and the first two mentioned lack any independent existence where they might experience the vicissitudes of the environment. In their host relations, we find them adapted to grasses which have been considered to be closer than the majority to the most ancient grasses. With hygrophilous grasses of the Paniceae in the tropics there is associated a group of ergots characterised by subglobose, light-coloured sclerotia. *Claviceps paspali* on *Paspalum*, *C. lulea* on *Panicum* and *Paspalum*, *C. queenslandica* on *Paspalum*, and *C. hirtella* on *Eriochloa*, *Paspalidium* and *Brachiaria* exemplify this group. These ergot species face periodic host dormancy but do not meet with the extreme conditions of cold or desiccation which prevail in other habitats. Ecologically they are intermediate between the ergots of moist tropical forest and those of areas with great seasonal changes of climate. The species of *Claviceps* with dark-coloured, elongated sclerotia are, in general those found on the more advanced grasses, i.e., grasses which have become adapted to habitats removed from the ancient, warm, moist forests. A group of ergots of this type occurs on Andropogoneae, a tribe which is characteristic of extensive tropical grasslands with marked dry seasons. *Claviceps purpurea* which ranges over most tribes of the Pooideae in a variety of habitats in temperate regions and where a long dormant phase in the hosts occurs, is the best known species of this group.

The present-day wide distribution of *Claviceps*, species of which occur in all continents, is evidence of the early differentiation of the genus from ancestral forms. From what has

been said of the history of the grasses, from the evidence of host relationships of present day species, from the ecological adaptations of sclerotia of ergot species, and from the morphology of the *Claviceps* species, we may postulate that the genus *Claviceps* is of tropical origin. The most primitive of its species existing to-day are found in moist tropical forest regions on hosts with primitive features. The more advanced ergots, those with sclerotia which can withstand the adverse conditions prevailing during their dormancy, may have evolved as the grasses spread out in past ages from the contracting region of moist tropical forest. *Claviceps pusilla*, with its wide distribution on Andropogoneae in the tropics and sub-tropics of the Old World, and *Claviceps purpurea* widely distributed on Pooideae throughout North Temperate regions occur in ecologically advanced habitats and their hosts include the grasses which have shown the greatest morphological advance. Their distribution suggests they are relatively old species, and this, considered with their advanced features, lends weight to the general conception of *Claviceps* as an old group with a long history.

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